HABITAT ASSOCIATIONS OF BREEDING BIRDS IN COTTAGE AND NATURAL AREAS OF CENTRAL ONTARIO

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Limited information is available about the habitat relationships of forest-breeding birds in central Ontario where, in the last 25 years, increasing cottage development has led to widespread habitat alterations. Several studies have examined avian responses to habitat changes caused by logging (Kilgore 1971, Webb et al. 1977). These areas, however, were allowed to revert to forest succession so the alterations were temporary. Cottage development results in major, long-term habitat alterations: the natural vegetation is changed substantially, although complete removal does not often occur, and undisturbed forest patches are left between lakes. Whitcomb (1977) predicted that regional extinction of avian species would be common with the removal and fragmentation of forests. The species most vulnerable to extinction are neotropical migrants (Whitcomb 1977), the most common breeding species in central Ontario forests.

In managing cottage development along lakeshores it is important to know how avian habitat is changed by human activity. The water/land interface is a unique habitat containing both coniferous and deciduous trees while back-shore areas are largely deciduous. The diversity provided by these areas adds to diversity of the larger vegetation community. Cottage development may reduce the diversity of vegetation over large areas much as agricultural activity has reduced the deciduous forest region into islands of woodlots throughout a sea of agriculture. The goal of this work was to provide managers with a detailed understanding of avian habitat requirements in Ontario in natural and cottage areas, and to determine what variables are important in describing the habitat associations. These results are necessary to develop an index of habitat disturbance that can be used to measure potential changes in avian species composition along lakeshore planned for cottage development.

Based on the conclusion that the configuration of the habitat is a major factor influencing habitat selection in birds (MacArthur and MacArthur 1961, MacArthur et al. 1962, Hilden 1965, Anderson and Shugart 1974), various multi-variate analyses can be used to quantify habitat relationships among species (James 1971, Holmes et al. 1979). These analyses indicate which habitat characteristics vary with the occurrence of each species and allow descriptions of avian habitat associations. Although other studies have used a similar approach, no data exist for birds in the Great Lakes/
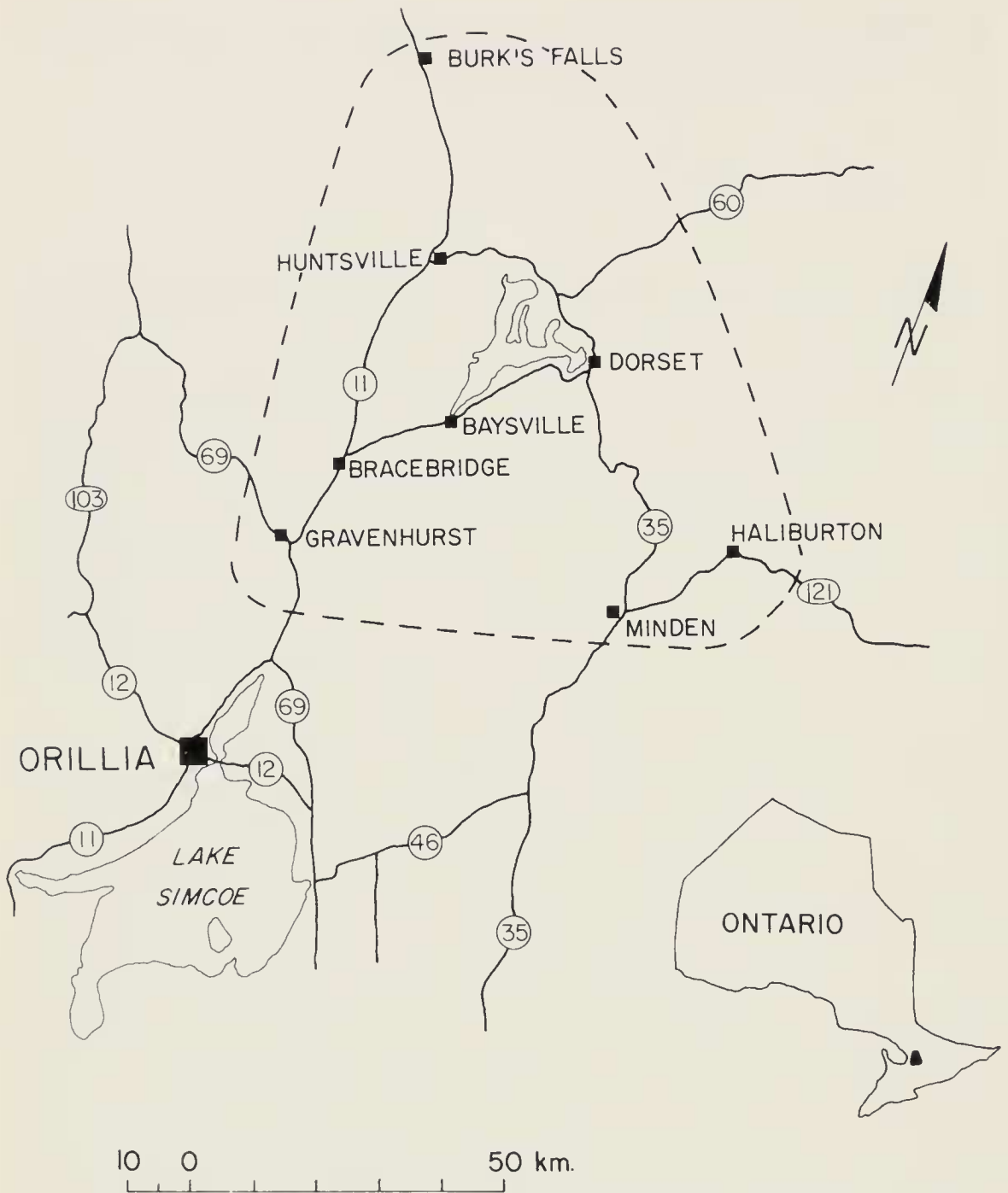
FIG. 1.   The area in Muskoka and Haliburton encompassed in the present study.

St. Lawrence forest region. This work is one part of the larger Lakeshore Capacity Study being conducted by the Ontario government, which is investigating the impact of cottage development on other wildlife species as well.

STUDY AREA

The study was conducted in the Muskoka and Haliburton districts of central Ontario (Fig. 1). The area is comprised primarily of rolling, forested terrain with many lakes and rivers

TABLE 1
Vegetation Variables Used in the Analysis of Nest-sites and Singing Posts

Mnemonics	Description
CANVOL	canopy volume (TVOL × CANHT)/10[a]
TVOL	percent tree volume
TCOV	tree coverage[a]
CANHT	canopy height
TIND	number of tree individuals
TREE 1	number of trees 8–16 cm DBH[a]
TREE 2	number of trees 16.1–24 cm DBH[a]
TREE 3	number of trees 24.1–32 cm DBH[a]
TREE 4	number of trees 32.1–40 cm DBH[a]
TREE 5	number of trees 40.1 + cm DBH[a]
TSP	number of tree species[a]
PCCT	percent conifer composition of the trees[a]
TSNAG	number of tree snags
SVOL	percent shrub volume
SCOV	shrub coverage[a]
SHIND	number of shrub individuals
SHSP	number of shrub species
PCCSH	percent conifer composition of the shrubs
SHSNAG	number of shrub snags
GVOL	percent ground volume
GCOV	ground coverage
FHD	foliage height diversity[b]

[a] Variables used in the discriminant function analysis.
[b] Based on MacArthur and MacArthur (1961).

which have been subjected to varying intensities of cottage development. Some lakes are inaccessible by road, and the vegetation has not been extensively altered. Other lakes are circled by a road, a transmission line right-of-way, and a continuous band of cottages so that much of the natural vegetation has been removed.

The study area is located in the ecotone between the boreal and the eastern deciduous forests. It is characterized by a mixture of white pine (*Pinus strobus*), balsam fir (*Abies balsamea*), and eastern hemlock (*Tsuga canadensis*), particularly along north-facing shorelines. Sugar maple (*Acer saccharum*) and red maple (*A. rubrum*) are common along south-facing shorelines, white birch (*Betula papyrifera*) and white cedar (*Thuja occidentalis*) within 10 m of shore, and beech (*Fagus grandifolia*) and yellow birch (*Betula lutea*) more than 20 m from shore.

METHODS

Seventy-three lakeshore study plots, 100 × 100 m each, were selected to represent a wide range of cottage development and habitat types in the area. The plots ranged from completely undeveloped or natural to areas with the highest density of cottages available, about one cottage per 15 m of shoreline. In 1977 and 1978 singing males were censused by the spot map method (Kendeigh 1944) for 4 h between 05:00 and 11:00. The census was repeated

TABLE 2
SPECIES AND SAMPLE SIZES USED IN THE ANALYSIS OF NEST-SITES AND SINGING POSTS AND THE CORRESPONDING SYMBOLS USED IN FIGS. 1–4[a]

Symbol	Species	Singing posts N	Nests N
PHOE	Eastern Phoebe (*Sayornis phoebe*)	27	10
LFLC	Least Flycatcher (*Empidonax minimus*)	30	6
EWPE	Eastern Wood Pewee (*Contopus virens*)	18	—
ROBN	American Robin (*Turdus migratorius*)	30	10
SWTH	Swainson's Thrush (*Catharus ustulata*)	21	—
VEER	Veery (*Catharus fuscescens*)	30	12
REVI	Red-eyed Vireo (*Vireo olivaceus*)	30	10
BWWA	Black-and-White Warbler (*Mniotilta varia*)	30	—
YRWA	Yellow-rumped Warbler (*Dendroica coronata*)	30	5
BTGR	Black-throated Green Warbler (*Dendroica virens*)	30	—
BTBW	Black-throated Blue Warbler (*Dendroica caerulescens*)	30	6
BBWA	Blackburnian Warbler (*Dendroica fusca*)	30	—
OVBD	Ovenbird (*Seiurus aurocapillus*)	30	7
ARMS	American Redstart (*Setophaga ruticilla*)	—	13
SOSP	Song Sparrow (*Melospiza melodia*)	30	—
WTSP	White-throated Sparrow (*Zonotrichia albicollis*)	30	—
RBGB	Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	30	9
YBSS	Yellow-bellied Sapsucker (*Sphyrapicus varius*)	—	12
BWHA	Broad-winged Hawk (*Buteo platypterus*)	—	9

[a] Species with a sample size smaller than nine were not used in the DFA.

three times between May 26 and July 20. Locations of any nests within these plots were also recorded.

Table 1 lists 22 vegetation variables which were measured, using a modification of the rangefinder method (Anderson and Shugart 1974), in 0.04-ha circular plots centered either on a singing post of a territorial male or on a nest. Since it was not possible to describe the singing posts of all species (Table 2), the species sampled were chosen to represent the range of available habitat. For 12 species, samples of sufficient size to allow measurements at nest-sites were obtained (Table 2).

Principal component analysis (PCA) (Anderson 1958, Morrison 1967) with varimax rotation was used to obtain ordinations of the species along vegetational gradients. The theory and ecological application of the PCA has been discussed elsewhere (James 1971, Gauch and Whittaker 1972). Although unequal sample sizes among species may weight the data in favor of the over-represented species, it was decided that more information would be lost by either reducing the sample size of all species to the same number as the most poorly represented species or to eliminate those species with smaller numbers. Singing posts and nest-sites were analysed separately. All 22 vegetation variables were used in each analysis. The BMD-P4M (Dixon 1975) computer program was used. An ordination was obtained by plotting the mean factor score for each species on the first three principal component axes.

A stepwise discriminant function analysis (Dixon 1975, BMD-P7M) was used to determine which of the vegetation variables are important in discriminating between species habitat

TABLE 3

SUMMARY OF THE RESULTS OF THE PRINCIPAL COMPONENT ANALYSIS OF 22 VEGETATION
VARIABLES FOR 16 BREEDING BIRD SPECIES' SINGING POSTS

Vegetation variable	Component correlations to original variables		
	1[a]	2	3
Canopy volume	0.941	0.0	0.0
Percent tree volume	0.868	0.0	0.0
Tree coverage	0.841	0.0	0.0
Canopy height	0.709	0.0	0.0
No. tree individuals	0.0	0.859	0.0
No. trees 8–16 cm DBH	0.0	0.811	0.0
No. trees 16.1–24 cm DBH	0.0	0.797	0.0
Tree species	0.0	0.503	0.0
Ground volume	0.0	0.0	0.848
cover	0.0	0.0	0.792
Shrub species	0.0	0.0	0.709
individuals	0.0	0.0	0.627
volume	0.0	0.0	0.0
cover	0.0	0.0	0.0
Confier composition shrubs (%)	0.0	0.0	0.0
Conifer composition trees (%)	0.0	0.0	0.0
No. trees 24–32 cm DBH	0.0	0.374	0.0
No. trees 32.1–40 cm DBH	0.285	0.0	0.0
Shrub snags	0.0	0.0	0.0
Tree snags	0.0	0.276	0.0
Foliage height diversity	0.380	0.0	−0.253
No. trees >40 cm DBH	0.455	−0.256	0.0
% of variance explained	21.1	13.8	10.5
Cumulative % variance explained	21.1	34.9	45.4

[a] The rows have been rearranged so that for each successive factor, loadings >0.50 appear first; loadings <0.25 have been replaced by zero.

associations (James 1971). If these variables are the same as those represented as important by the PCA, and the resulting distribution of species along the discriminant function axes are similar to those along the PCA axes, then the habitat variables designated as contributing significantly to variation by both analyses should be good predictors of avian habitat association (Smith 1977, Whitmore 1977, Holmes et al. 1979).

RESULTS

Principal component analysis.—The first three components of the PCA of singing posts explained 45% of the total variance in the data set. Only these three components are treated here since the remaining components each explained substantially smaller amounts of the total variance.

The first principal component for singing posts accounted for 21.1% of the total variance, and was highly correlated with canopy volume, tree

TABLE 4

SUMMARY OF THE RESULTS OF THE PRINCIPAL COMPONENT ANALYSIS OF 22
VEGETATIONAL VARIABLES FOR 12 BIRD SPECIES' NEST-SITES

Vegetation variable	Component correlations to original variables		
	1[a]	2	3
Canopy volume	0.913	0.0	0.0
Tree volume	0.862	0.291	0.0
Tree coverage	0.832	0.0	0.0
Canopy height	0.795	0.0	0.0
No. trees 32.1–40 cm DBH	0.575	0.0	0.0
No. trees >40 cm DBH	0.549	0.0	0.0
Foliage height diversity	−0.509	−0.333	0.0
No. tree individuals	0.0	0.922	0.0
No. trees 8–16 cm DBH	0.0	0.886	0.0
No. trees 16.1–24 cm DBH	0.0	0.829	0.0
Ground volume	0.0	0.0	0.880
No. shrub individuals	−0.281	−0.288	0.795
Shrub species	0.0	0.0	0.746
Ground cover	0.319	0.0	0.729
Shrub volume	0.0	0.0	0.0
Shrub snags	0.0	0.0	0.0
Shrub cover	0.0	0.0	0.394
Conifer composition trees (%)	0.0	0.0	0.0
Confier composition shrubs (%)	0.0	0.0	0.0
Tree species	0.0	0.425	0.0
Tree snags	0.0	0.501	0.0
No. trees 24.1–32 cm DBH	0.422	0.359	0.0
% variance explained	26.3	14.5	11.1
Cumulative % variance explained	26.3	40.8	51.9

[a] The rows have been rearranged so that for each successive factor, loadings >0.50 appear first; loadings <0.25 have been replaced by zero.

volume, tree cover, and canopy height (Table 3). Birds found in mature forests with a dense canopy had high scores on this component. Species found in the open habitats of highly developed areas where most of the large trees had been removed had low values on this component. The second principal component accounted for 13.8% of the total variance, and was highly correlated with number of tree individuals, number of trees (8–16 cm), and number of trees (16–24 cm). Species found in early successional forests where there were many small trees, as along the edge of cottage clearings, had high scores on this component. Intermediate scores on this component coincided with undisturbed mature forests, whereas low scores coincided with open areas and disturbed forest habitats where
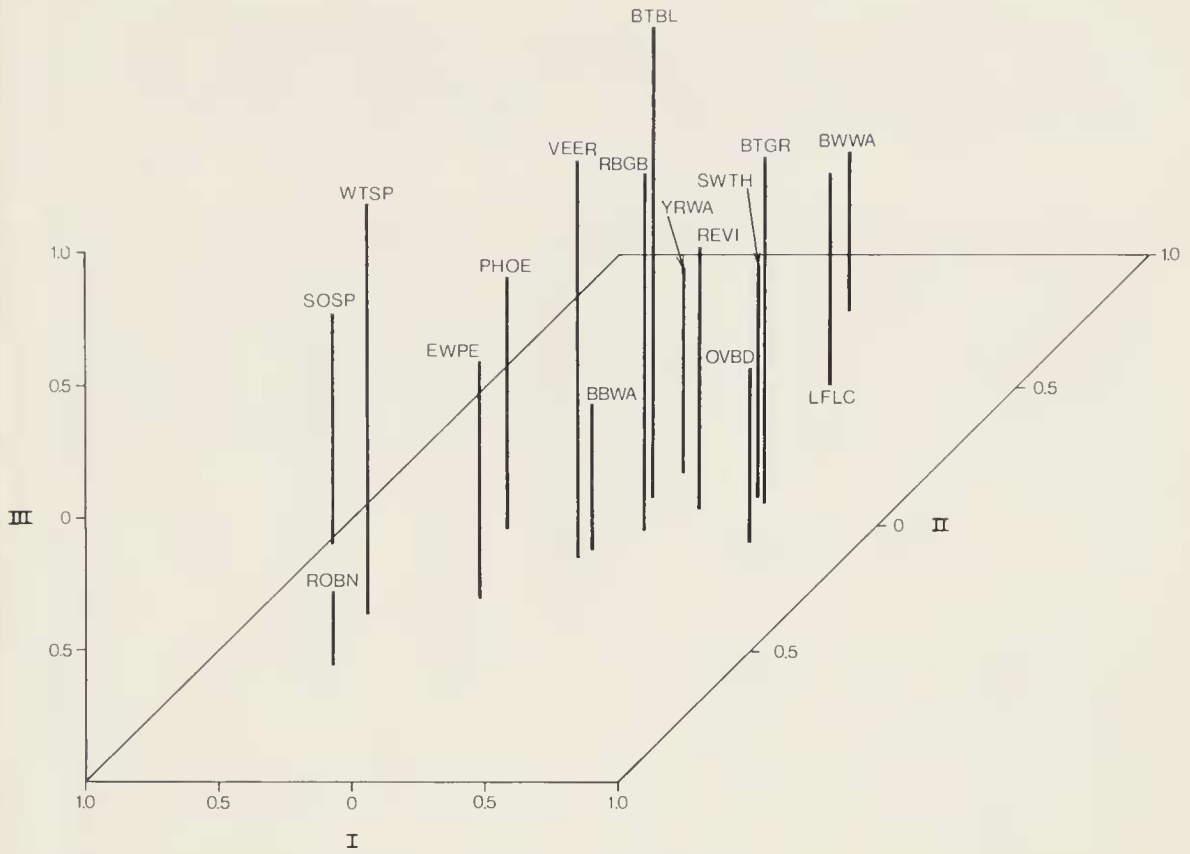
FIG. 2. Representation of the first three axes of the habitat ordination of bird species' singing posts. A description of each axis is given in the text.

most of the trees had been removed. The third component accounted for 10.5% of the total variance, and was highly correlated with ground volume, ground cover, number of shrub species, and number of shrubs. Species associated with high values of this component were found where there was a dense understory, as along forest edges, transmission lines, and road rights-of-way. Species with low scores occurred in mature forest, especially coniferous woods, or where the understory had been cleared.

The results of the PCA of the variables measured at nest-sites were very similar to those at singing posts. The first three principal components included the same variables with slight differences in the order of importance (Table 4). Again, as with the singing posts, the first three components each explained a large portion of the total variance. Overall, the first three components for nest-sites accounted for 51.9% of the total variance.

Using the mean of the factor scores of all individuals of each species, a three-dimensional ordination of the species in habitat space was produced. The axes were described by the eigenvectors associated with the first three principal components. This allowed a visual presentation of
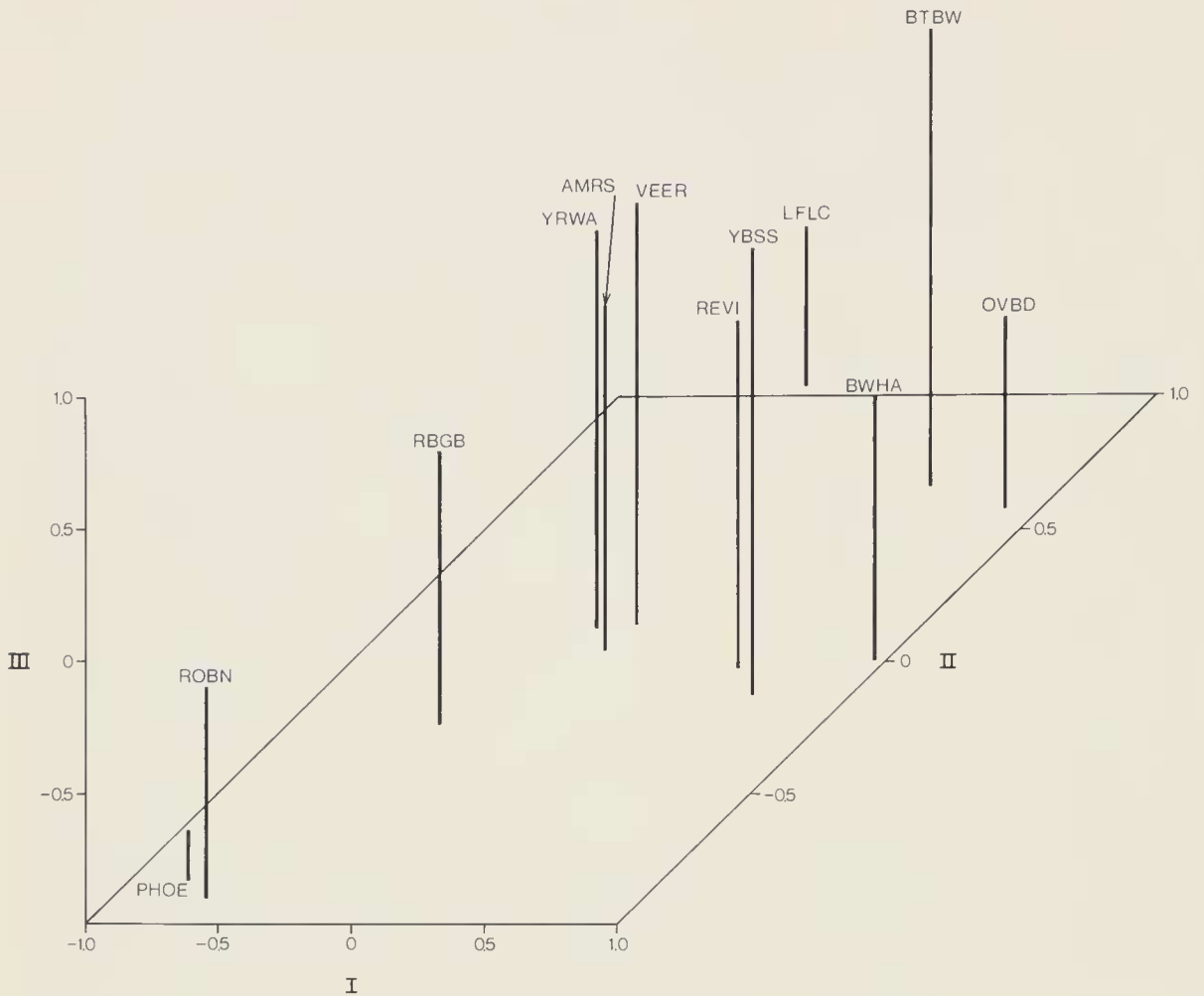
FIG. 3. Representation of the first three axes of the habitat ordination of bird species' nest-sites. A description of each axis is given in the text.

habitat relationships in which the distance from one species to another was proportional to the difference between them (Isebrands and Crow 1977).

Figures 2 and 3 show the habitat ordination of singing posts and nest-sites, respectively. The axes in both figures are associated with similar habitat characteristics. The first axis corresponds to increasing canopy volume and separates the open country birds from the forest birds. For singing posts, the Ovenbird, Swainson's Thrush, and Black-throated Green Warbler had high scores on this component, while the Song Sparrow, American Robin, and White-throated Sparrow had very low scores.

The second axis is associated with increasing tree density. For singing posts, the Black-and-White Warbler had the highest score on this axis while the robin had the lowest. For nest-sites, the Least Flycatcher, Black-throated Blue Warbler, and Ovenbird had very high scores while the robin and Eastern Phoebe had low scores.

The third axis is associated with increasing amount of understory. For

singing posts, the Black-throated Blue Warbler and robin scored at the high and low extremes of this component, respectively. For nest-sites, the Black-throated Blue Warbler and Yellow-bellied Sapsucker had very high scores while the Eastern Phoebe and Yellow-rumped Warbler had very low scores.

Discriminant function analysis.—The DFA requires that the number of variables not exceed the sample size of the smallest group. To meet this requirement, the number of vegetation variables was reduced to nine (Table 1) and any species with a sample size smaller than nine was eliminated (Table 2). The vegetation variables which were included in the DFA were selected to be indicative of the main habitat types and not to show high correlations with any of the former variables. Because of the high correlations among them, the three smallest size classes and the two larger classes for trees were summed to give a single measure of the number of small and large trees, respectively.

Four variables were chosen by the stepwise DFA to differentiate among singing posts of each species (Table 5). The absolute value of the coefficients indicated the relative contribution of each variable to the respective discriminant function axis. The number of small trees, and to a lesser extent, tree cover and percent conifer composition, were major contributors to the first discriminant function axis. Tree cover and ground volume were the major contributors to the second and third axes, respectively. An ordination of the species' means along the first three discriminant function axes is shown in Fig. 4.

Shrub cover was the only variable entered in the stepwise DFA of nest-sites. A line graph was drawn to illustrate the ordination of species along this axis (Fig. 5).

DISCUSSION

Important habitat characteristics.—To understand the effect of cottage development on avian communities it is necessary to know what habitat characteristics are important in determining the distribution of breeding birds and to some extent understand why these habitat characteristics are important. Once these habitat characteristics are identified and the avian species associations with them are known, predictions can be made regarding the effects of habitat disturbances on the avian populations in an area.

The vegetation variables indicated by the PCA to be of great importance in describing the variation in this data set agree closely with similar studies by James (1971), Smith (1977), and Whitmore (1977), even though different avian communities and habitats were studied in each case (Table 6). The first two principal components of our study and Smith's (1977) both describe habitat variables associated with canopy and tree density. James'

TABLE 5

STANDARDIZED DISCRIMINANT FUNCTION COEFFICIENTS FOR THE FIRST THREE
DISCRIMINANT FUNCTIONS FOR 15 SPECIES' SINGING POSTS[a]

Vegetation variable	Discriminant function		
	I	II	III
No. of trees 8–32 cm DBH	−0.0436	0.0168	0.0361
% tree coverage	−0.0410	0.0812	−0.0226
Ground volume	−0.0159	−0.0004	−0.0939
% conifer composition of trees	−0.0383	−0.0152	−0.0016

[a] Variables used in the analysis are indicated in Table 1.

(1971) and Whitmore's (1977) results describe similar vegetation charac-
teristics to our study and Smith's (1977), although there are some differ-
ences in the order of importance of variables to each component. This can
be attributed to differences in the range of vegetation variables sampled
in each study. James (1971) sampled mainly deciduous woods in Arkansas
in which there were a large number of tree species with a range of heights.
Whitmore (1977) sampled open field and forest in Utah of relatively uni-
form height and dominated by only two tree species. Smith (1977) sampled
a forest moisture gradient in Arkansas along which there was a variety of
deciduous tree species. Our study included shoreline with coniferous,
mixed, and deciduous forest as well as forest altered by cottage develop-
ment. The lower proportion of total variance explained in our study and
that of Smith's (1977) in contrast to that explained by James (1971) and
Whitmore (1977) can be attributed in part to their use of mean values for
each vegetation variable for each species, fewer vegetation variables, and
their sampling of a more restricted range of habitat types.

In another study in Utah, Whitmore (1975) found the four most important
variables selected by the DFA were percent canopy cover, percent shrub
density, number of small trees, and percent ground cover. With the ex-
ception of percent conifer composition which was not considered in Whit-
more's (1975) study, his results are comparable to ours. Canopy cover was
also found to be the most important variable in a similar study done in
Arkansas by James (1971), although her results differed for other variables.

The close similarity of the PCA for song posts and nest-sites further
indicates the importance of canopy volume, tree density, and amount of
understory in the distribution of individuals throughout the habitat. This
similarity also suggests that these vegetational characteristics may be of
general significance with regard to satisfying different habitat require-
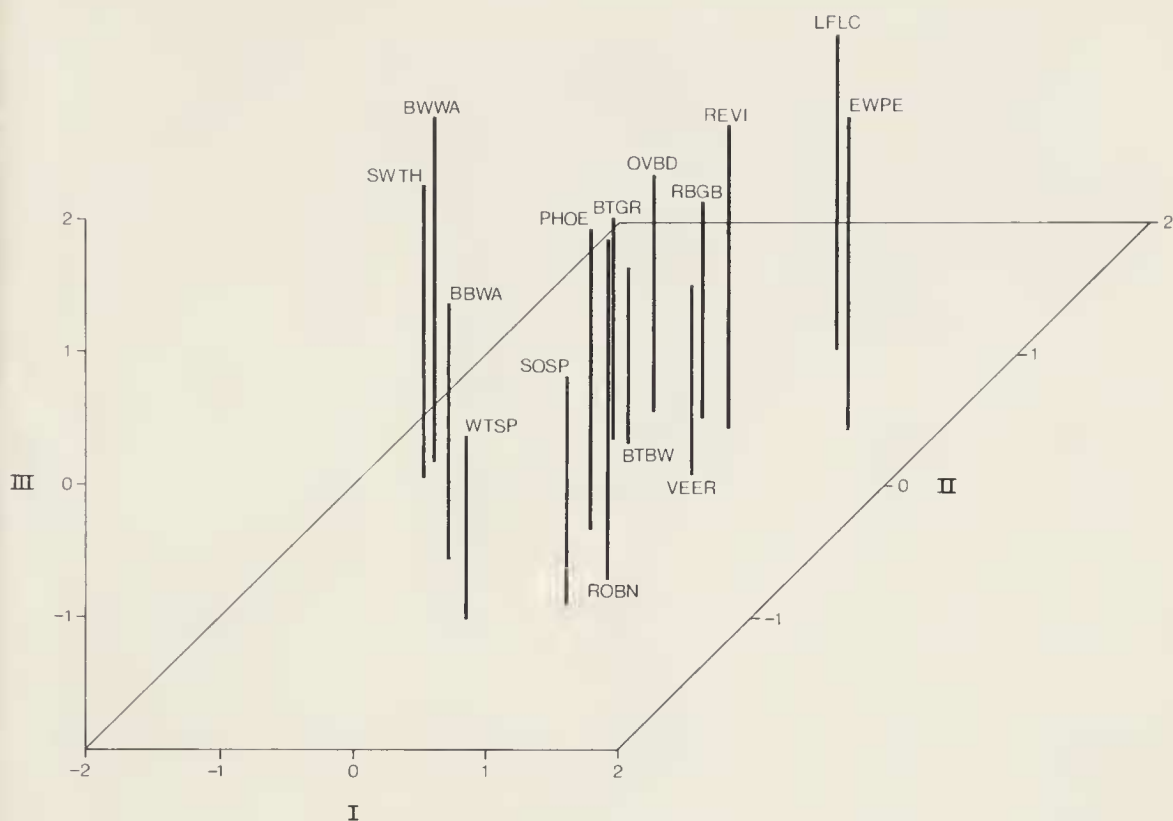ments of different avian species.

FIG. 4. Ordination of bird species' singing posts along first three discriminant function axes. A description of each axis is given in the text.

Avian habitat selection is considered to be primarily based on proximate factors involving the general vegetative structure, substrate, and terrain (Holmes et al. 1979, Rotenberry and Wiens 1980). The consistent importance of canopy volume, tree density, and amount of understory in our analyses as well as those of James (1971), Whitmore (1975), and Smith (1977) suggests that these vegetational characteristics may be important in terms of specific search images used by birds for habitat selection. There are several possible reasons why these vegetation variables may be important in predicting avian habitat associations.

The canopy layer is important because it adds vertical structure to the habitat providing another dimension for potential food sources, nest-sites, and shelter from predators and inclement weather (Franzreb 1976, Holmes et al. 1979). Willson (1974) found that the greatest variation in species composition occurred when the canopy layer was added to a habitat. Canopy volume has been shown (Morse 1971) to predict the habitat selection of spruce-dwelling wood warblers (Parulinae). Sturman (1968) found that canopy volume was associated with the relative abundances of two chickadee (*Parus* spp.) species.

Tree density or the number of small trees may be an important measure

RHOE

2.0 —

1.5 —

1.0 —

0.5 —|— ROBN

0 —|— YBSS
   | AMRS

    — BWHA
    — REVI
-0.5 —

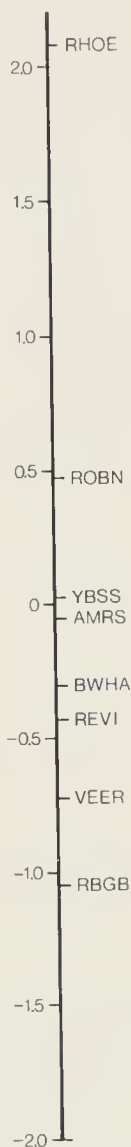   — VEER

-1.0 —|— RBGB

-1.5 —

-2.0 —|—

FIG. 5.   Ordination of bird species' nest-sites. This axis describes a gradient of increasing shrub cover.

of relative tree size. Tree size may be important in habitat selection because of preferences of some species for certain trunk diameters and heights for singing posts, foraging, and nest-sites (Morse 1967, 1968; Dickson and Noble 1978).

The effect of vegetation ground volume on species distribution may be explained by Roth's (1976) suggestion that increasing ground and shrub volume results in greater spatial heterogeneity. Coniferous composition may be important as another measure of horizontal structuring of the habitat, since conifers provide both an inner and outer layer for which particular species are specialized (MacArthur 1957). Studies relating species diversity to foliage height diversity (MacArthur 1957) have been inconsis-

TABLE 6

COMPARISON OF THE RESULTS OF THE PRINCIPAL COMPONENT ANALYSIS WITH PUBLISHED STUDIES

	This study	James 1971[a]	Whitmore 1977[a]	Smith 1977
PC I	CANVOL TVOL TCOV CANHT	TSP TCOV TREE 2 TREE 1 CANHT	GCOV TREE 3	TCOV[b]
PC II	TIND TREE 1 TREE 2	SHIND/4	SHIND	TREE 2[c]
% total variance explained by PC I and PC II	35	77.3	73.5	32.2
No. of bird species	15	46	24	8
No. variables	22	10	10	25
Study area	central Ontario: forests, cottaged lots	Arkansas: forests, wetlands	SW Utah: cottonwood forest, wetlands, farmland	NW Arkansas: forest moisture gradient

[a] PCA was performed using the mean of each habitat variable for each species.

[b] This principal component also includes number of post oak <22.9 cm DBH, number of black hickory, number of post oak >22.9 cm DBH.

[c] This principal component also includes number of shagbark hickory, number of beech >22.9 cm DBH.

tent, which suggests that other factors must influence species distribution (Balda 1969, Kilgore 1971, Stamp 1978, Holmes et al. 1979).

Shrub cover may be important in nest-site selection because it could determine different types of concealment from predators and the amount of protection from inclement weather. Shrub cover has been found by Bertin (1977) to be the single most important factor that distinguishes Wood Thrush (*Hylocichla mustelina*) from Veery territories. Kilgore (1971) found that removal of the ground and lower shrub layers can result in changes in species composition of these layers but does not affect the canopy layer. Since all species examined except the Broad-winged Hawk were found to nest in the ground or shrub layers, other habitat characteristics could have been important if more canopy nesters had been included.

As Holmes et al. (1979) have recently shown, patterns of avian distribution are also influenced by forest plant species composition. In the man-

agement of habitat for a variety of purposes, plant species composition has to be considered in addition to the structural features considered in this study.

Effects of cottage development.—By interpreting the positions of each species along the principal component and discriminant function axes, habitat associations and a species' response to cottage development can be described. The White-throated Sparrow, Song Sparrow, and American Robin were associated with habitats typified by low canopy volume and tree density, shrubby areas and lawns in highly developed habitats. The White-throated Sparrow, usually considered a boreal forest bird (Kendeigh 1948, Martin 1960) was associated with high coniferous composition and dense understory. Its preference for an open canopy with a well-developed understory makes it well suited to inhabit cottaged lots in coniferous woods where most of the tree layer has been removed. The Song Sparrow was associated with mixed conifer composition and a reduced understory found in cottaged areas where much of the vegetation had been removed. The robin, often found in urban areas (Howell 1942, Young 1955, Howard 1974), was associated with very low ground volume and mixed coniferous composition for its singing posts and similar habitat with low shrub cover for its nest-sites. Its ability to nest on drainpipes and ledges and its preference for open areas for foraging allows the robin to be successful in highly developed areas where most of the natural vegetation has been removed.

The phoebe and Eastern Wood Pewee were associated with slightly higher canopy volume and tree density, features indicative of the periphery of a clearing. Both the phoebe and pewee require an open area for fly-catching (Hespenheide 1971, Kilgore 1971) and some canopy for perching. The phoebe's preference for low shrub cover and its ability to find nest locations on buildings makes it able to inhabit cottaged lots with small clearings which allow for adjacent nesting and foraging habitat. Hespen-heide (1971) classified the pewee as an edge species, since the main cri-terion for its presence is a discontinuity in the canopy layer in close prox-imity to open areas for foraging and trees for perches and nest-sites. The pewee could be found on the forest edges of cottage clearing regardless of lot size.

Although the Blackburnian Warbler and Veery belong to different feed-ing guilds, they were both associated with intermediate canopy volume and slightly less than mean tree density. The Blackburnian Warbler was found in coniferous woods with little understory. It is usually associated with a high canopy for foraging (Griscom and Sprunt 1957, Morse 1976) suggesting that it is found on cottage lots in mature woods where the canopy layer has not been disturbed or in undisturbed forests. The Black-burnian Warbler is negatively affected by even low levels of disturbance

(Webb et al. 1977), probably because this species forages among outer twigs and branches of trees (Holmes et al. 1979).

The singing posts of the Veery were in deciduous woods with a well-developed understory. Nest-sites were associated with intermediate canopy volume, tree density, and very high shrub coverage as found by Bertin (1977) as well. The Veery would be expected to benefit from a pattern of tree removal in mature forests where the understory was not disturbed, resulting in greater shrub cover and development of the understory.

The Black-throated Blue Warbler, Yellow-rumped Warbler, and Red-eyed Vireo were associated with intermediate levels of canopy volume and tree density indicative of selective tree removal in mature woods or of immature woods, which in our study area were usually associated with forest succession on cleared lots. The Black-throated Blue Warbler was found in mixed or deciduous woods with moderate canopy volume and tree density. The Black-throated Blue Warbler requires a greater amount of understory. Webb et al. (1977) found that removal of the tree layer did not change the population density of the Black-throated Blue Warbler which suggests that disturbance of the canopy layer should not affect its nesting habitat. Although the Black-throated Blue Warbler forages among the outer twigs and branches of trees (Holmes et al. 1979), it is capable of using a variety of canopy heights and volumes.

The Yellow-rumped Warbler was associated with mixed woods with some understory. This species has been shown to exhibit a high degree of plasticity in habitat preferences for foraging and nesting (Ficken and Ficken 1967, Morse 1971, Franzreb 1976, Dickson and Noble 1978), and is dependent to some extent on competitive displacement (Morse 1976).

The Red-eyed Vireo was associated with deciduous woods with some understory for singing posts and nest-sites. The Red-eyed Vireo has been found to tolerate varying degrees of tree removal (Webb et al. 1977), since it has been reported in habitats ranging from dense shrub to mature forest (Kendeigh 1948, Rice 1978). Conner and Adkisson (1975) and Adams and Barrett (1975), however, found the Red-eyed Vireo intolerant of tree removal, suggesting that in some areas other factors such as competitive interaction may be important in the habitat selection of this species.

The singing posts of the Rose-breasted Grosbeak were associated with deciduous woods with a dense understory. Nest-sites had a low canopy volume and very high shrub cover typical of immature trees where this species has been noted to nest in other parts of its range (Kendeigh 1946, 1948; Kricher 1973). The preference for high tree density and extensive shrub cover leads the Rose-breasted Grosbeak to inhabit areas where large trees have been removed and the understory has been allowed to develop (Webb et al. 1977, Possardt and Dodge 1978).

The Swainson's Thrush, Black-throated Green Warbler, and Ovenbird were associated with high canopy volume and intermediate tree density indicative of undisturbed forests. The Swainson's Thrush was associated with high conifer composition and little understory. There is little information available about the nesting habitat of this species. Its association with mature woods suggests an intolerance of any habitat alteration. Webb et al. (1977), however, found that it was not affected by intense logging. Since the Swainson's Thrush nests in the shrub layer, habitat alterations affecting this stratum may be more critical to its occurrence.

The Black-throated Green Warbler was associated with coniferous, mature woods with considerable understory. MacArthur (1958) and Morse (1971) noted a high degree of stereotypy in habitat utilization, leading to narrow habitat use for this species. These specialized habitat requirements would explain its limitation to undisturbed coniferous woods (Morse 1976, Webb et al. 1977).

The Ovenbird was associated with mixed woods with little understory, typical of undisturbed mature forests. Several studies have indicated population declines with tree removal (MacClintock et al. 1977, Whitcomb et al. 1977, Conner and Adkisson 1975), although Adams and Barrett (1976) found a population increase. The Ovenbird would be expected to be found near cottaged lots in mature woods if human activity did not disturb this ground nesting species.

The Black-and-White Warbler and Least Flycatcher were associated with high tree density and high canopy volume, typical of an area which had been cleared and allowed to proceed to an early successional forest stage. Although the Black-and-White Warbler is considered to be a deciduous forest bird (Harrison 1975), it was associated with high conifer composition in our study area. Since it is a ground nester, it would not be expected to tolerate extensive human activity. Possardt and Dodge (1978) have shown that disturbance of the understory results in a population decline.

The singing posts and nest-sites of the Least Flycatcher were associated with deciduous woods. The Least Flycatcher is a forest bird found near openings in the canopy (Kendeigh 1948, Breckenridge 1956, Hespenheide 1971). Mature forests subject to selective tree removal to open the canopy should provide favorable habitat, whereas extensive tree removal or reduction of the understory should create unsuitable habitat for this species (Webb et al. 1977, Possardt and Dodge 1978).

The PCA and DFA proved reliable in determining avian habitat relationships and the effects of habitat alterations on avian distributions. The information obtained compared favorably with studies involving extensive, long-term data collection (Bertin 1977, Webb et al. 1977, Rice 1978).

The implications of the results of the DFA and PCA are threefold. First, reasonably accurate measures of species habitat relationships can be obtained by measuring only four habitat characteristics: canopy volume, tree density, shrub coverage, and percent conifer composition. A manager, wanting to understand how the habitat of birds breeding in an area is changed by habitat disturbance, can measure these four habitat characteristics and learn a great deal about the magnitude of the disturbance.

Second, DFA and PCA can be used to establish the importance of separate habitat characteristics in avian habitat associations. The impact of cottage development on breeding birds can then be predicted by measuring how cottage construction changes the vegetation. These effects are dependent on the amount of habitat destruction in building on a cottage lot. For example, a cottager on a deciduous lot who selectively removes only a few trees and leaves the ground or shrub layers intact would encourage Veery nesting in the area but deter Ovenbirds.

Third, since only four habitat characteristics are required to establish avian habitat associations, a simple index of habitat disturbance caused by cottage development can be developed to measure effects on avian communities based on the amount of change in the four habitat characteristics. Although the development of an index of habitat disturbance is not discussed here, it was necessary to establish what variables would be useful in developing the index as well as determining how these habitat variables are related to avian habitat associations.

SUMMARY

Habitat associations of breeding birds in central Ontario were determined by measuring habitat characteristics at singing posts and nest-sites and by using these variables in principal component and stepwise discriminant function analyses. These results were then used as baseline data to predict avian responses to habitat disturbance caused by cottage development. Three habitat variables were important in accounting for large proportions of the total variance in all analyses. These were canopy volume, tree density, and amount of understory. The consistent importance of these variables in our analyses as well as in other published studies suggests that these variables may be significant in avian habitat selection. Coniferous composition was important in the discriminant function analysis, and may be important as another measure of horizontal structuring of habitat. By interpreting the positions of each species along the discriminant function and principal component axes, habitat associations could be described and predictions made regarding the response of a species to habitat disturbance caused by cottage development.

In Muskoka-Haliburton removal of the majority of vegetation around a cottage leaves breeding habitat for Song Sparrows and robins. If some predominately coniferous vegetation is left, White-throated Sparrows will also occur. Phoebes and pewees occur on the periphery of cottage clearings. Selective tree removal while leaving the rest of the vegetation undisturbed would create breeding habitat for Veerys, Black-throated Blue and Yellow-rumped warblers, and Red-eyed Vireos. Cottage lots that have been cleared and allowed to go through natural succession to the immature tree stage would create breeding habitat for Rose-breast-

ed Grosbeaks. Swainson's Thrush, Black-throated Green and Black-and-White warblers probably will not occur near cottages because they are intolerant of vegetation disturbance.

ACKNOWLEDGMENTS

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